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THE DISTRIBUTION OF THE CHONDRIOSOMES TO THE SPERMATOZOA IN SCORPIONS

By Edmund B. Wilson

DEPARTMENT OF ZOOLOGY, COLUMBIA UNIVERSITY

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The spermatozoon carries into the egg two kinds of bodies both of which have been supposed to play a definite part in heredity; these are the *chromosomes* and the *chondriosomes*, the former belonging to the nucleus, the latter to the protoplasm or cytoplasm. If these bodies are in fact concerned in heredity we should in general expect them to be equally distributed to the germ-cells by means of division or some similar process of equal allotment; and as far as the chromosomes are concerned such is always the fact, except in case of the sex-chromosomes.[1] The chondriosomes, too, are distributed with approximate equality in many cases, but whether they are comparable with the chromosomes in this regard has not yet been certainly determined. I have for some time been engaged with a study of this question in two species of scorpions in both of which the phenomena are displayed with almost unexampled clearness, and which seem to give a conclusive result on this point. It is in some respects a surprising one.

The two species in question are *Opisthacanthus elatus* (Gervais) from Southern California and *Centrurus exilicauda* (Wood) from Southern Arizona.* In the latter, alone among animals hitherto examined, it is possible to conclude with certainty that the chondriosome-material is divided with exact equality among all the spermatozoa. The definiteness of this result is owing to the unique fact that before the maturation-divisions take place the whole of the chondriosome-material in the primary spermatocytes is concentrated in a single ring-shaped body which is then equally divided in such a way that each spermatid receives one-quarter of the products, the process taking place with a precision that is comparable to that seen in the distribution of the chromosome-material. The body in question represents a hitherto undescribed type of chondriosome. It arises from numerous minute mitochondria or chondrioconts which early in the growth-period of the spermatocytes become concentrated to form a large, homogeneous and sharply defined ring, lying in the protoplasm and surrounding the idiozome near one pole of the nucleus. Persisting unchanged throughout the growth-period this body places itself like a heterotype chromosome-ring in a position tangential to the first spermatocyte-spindle, elongates during the anaphases (fig. *a*) and then breaks apart at its polar apices, thus giving rise to two half-rings which quickly straighten out to form two similar and equal rods that lie side by side near and parallel to the spindle. Early in the telophase each rod becomes constricted at its middle point and then divides transversely (fig. *b*) into two equal parts which pass to opposite poles. Each secondary spermatocyte thus receives two equal daughter-rods (each a quarter of the orig-

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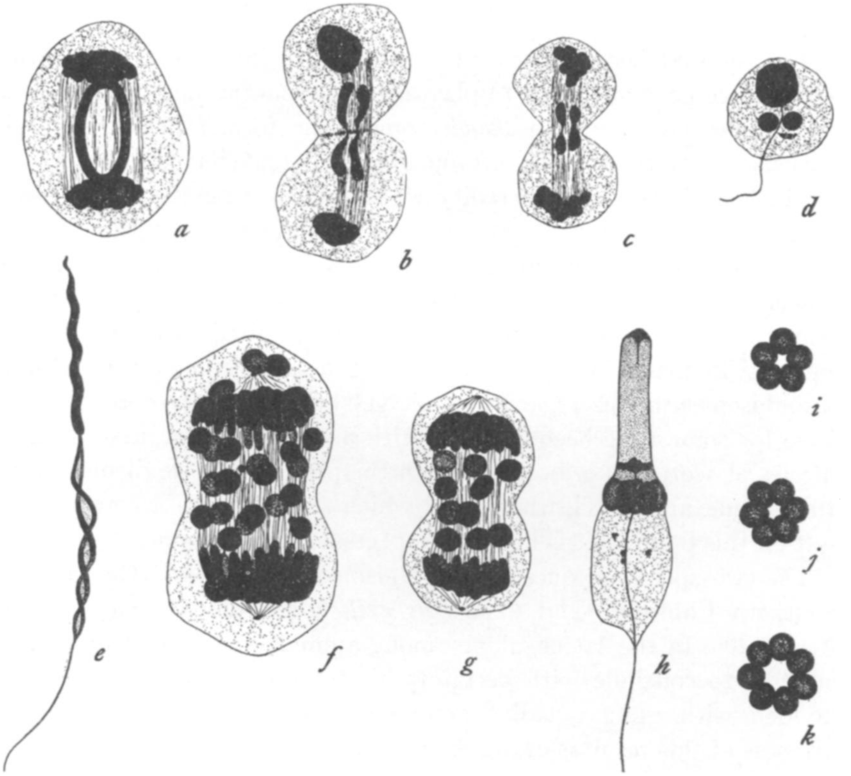
*My thanks are due to Nathan Banks, Esq., for an authoritative identification of the species.



a—e, Centrurus exilicauda (Wood)

a, first spermatocyte-anaphase, chromosomes at the poles, chondriosome-ring in typical position to divide; *b*, telophase, showing final division of the ring; *c*, second division telophase, chromosomes at the poles, final division of the chondriosome-rods; *d*, young spermatid with nucleus and double nebenkern; *e*, early stage of elongation and twisting of the double nebenkern to form the spiral envelope of the flagellum.

f—k, Opisthacanthus elatus (Gervais)

f, anaphase of first spermatocyte-division, *g*, of second division, showing rod-shaped chromosomes passing to the poles and the rounded chondriosome-spheres scattered about the spindle; 22 of the latter appear in the first case, 10 in the second (complete numbers are 24 and 12 respectively); *h*, early spermatid with ring of chondriosomes (nebenkern-organ) at the base of nucleus; *i, j, k*, polar views of the nebenkern-organ showing variation in number of chondriosome-spheres.

inal ring) which persist throughout the interkinesis and repeat the process in the second division, taking up a position near the spindle and dividing transversely at their middle points (fig. *c*). Each spermatid receives two of the final products, which give rise to a nebenkern consisting of two equal parts (fig. *d*), the axial filament growing out between them from a blepharoplast situated at the base of the nucleus. It thus comes to pass that each spermatozoon receives exactly two-eighths of the original ring (hence of the original chondrioma of the spermatocyte), the history of the chondriosome-ring suggesting in a general way that of a heterotype chromosome-ring, though its mode of division is very different in detail. In the later stages, which are of great interest, the two halves of the nebenkern assume the form of flattened rods which rapidly elongate backwards, at the same time twisting spirally around the axial filament (fig. *e*) until they finally extend throughout nearly the whole length of the flagellum and are converted into two very fine, closely twisted parallel fibrillae that form the spiral envelope of the tail. Each of these fibrillae, as is proved by its genesis, represents one-eighth of the original ring and hence of the spermatocyte-chondrioma.

Nothing could be more surprising than the contrast to the foregoing mode of chondriosome-distribution seen in *Opisthacanthus*. It should first be emphasized that the two species agree closely in respect to the origin, staining reactions and ultimate fate of the chondriosomes: they are derived from numerous minute chondrioconts; they stain characteristically by Benda's method; they give rise to the nebenkern and ultimately to the tail-envelopes. A most striking difference appears, however, in respect to the remaining phenomena which are in a general way in agreement with those described by Sokolow[2] in the European species *Euscorpius carpathicus*, though some important differences are seen. In place of the ring appear approximately 24 fairly large, separate, hollow spheroidal bodies scattered without discernible order through the protoplasm. These bodies, which may be called *chondriosome-spheres*, do not at any time during the maturation-process show evidence of division nor do they enter into definite relation with the spindle. Scattered irregularly about the latter (figs. *f*, *g*,) they are at each division segregated into two approximately equal groups, half of them passing into each daughter-cell; and during this process they seem to be quite inactive, being passively carried along in the protoplasm as the cell divides. Their total number is thus reduced approximately from 24 to 12 in the first division, and from 12 to 6 in the second. Each spermatid thus receives six chondriosome-spheres as a rule, but sometimes five or seven; and these ultimately arrange themselves in a ring shaped group to form a 'nebenkern-organ' lying at the base of the nucleus and surrounding the blepharoplast (centriole) and the outgrowing axial filament (figs. *h—k*). Two hundred cases thus far tabulated give 73% with six chondriosome-spheres, 16% with five and 11% with seven. Other numbers have not been observed.

The sperm thus passes through a stage in which it possesses a nebenkern closely similar to the definitive middle-piece of certain nemertines, pelecypods and annelids (Retzius); but this is only a temporary condition. Becoming closely applied to the axial filament, the ring of chondriosomes is in later stages progressively drawn out backwards to form the envelope of the flagellum, apparently extending as far as the end-piece of the latter. There are some indications that a remnant of the chrondriosome-ring may finally be cast off along with the general protoplasmic remnant which, as usual, is sloughed off from the elongating flagellum, but this has not yet been clearly established. I have not yet been able to determine whether the envelope develops a spiral structure analogous to that so clearly seen in *Centrurus*.

From the foregoing account it is evident that chondriosome-material having the same origin, fate and (presumably) physiological significance may be distributed to the germ-cells by processes widely different even in nearly related animals. In one of these scorpions the distribution is effected by a definite process of division, in the other by an operation that has at least the aspect of a hit-or-miss segregation, and one that gives only an approximate equality of result. On its face this would seem to indicate that a wide distinction should be drawn between chondriosomes and chromosomes in respect to their power of division and their relation to heredity. It is of course possible that in both the cases here described the chondriosomes may multiply by division at an earlier period (a point now under investigation). It may also be suspected that division of the chrondriosome–ring is not an independent or autonomous act but depends upon the division of other elements with which it is associated. In either case the facts raise interesting questions concerning the power of division on the part of the several cell-components and the relation of this power to the principle of genetic continuity in general.

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[1] Certain special exceptions, such as the supernumerary chromosomes or the unequal small bivalents of Orthoptera, are here disregarded since they are readily explicable in accordance with the general rule.

[2] *Arch. Zellforschung*, 9, 3, (1913).